

ECOLOGY AND CONSERVATION OF *ACACIA* AND *PROSOPIS* (FABACEAE) WOODLANDS OF THE MOJAVE DESERT, U.S.A.

Scott R. Abella¹ and Kenneth L. Chittick

Department of Environmental and Occupational Health

University of Nevada, Las Vegas

Las Vegas, Nevada 89154-3064, U.S.A.

abellaNRC@gmail.com

¹Present address: Natural Resource Conservation LLC, Boulder City, Nevada 89005, U.S.A.

ABSTRACT

Woodlands of *Acacia greggii*, *Prosopis glandulosa*, and *Prosopis pubescens* are of conservation-priority in the Mojave Desert because of their wildlife and watershed values. We measured plant community composition, environmental variables (e.g., slope gradient, soil), and ecological condition (e.g., tree recruitment) in 50, 0.1-ha woodland plots within 449,000-ha Lake Mead National Recreation Area in the eastern Mojave Desert in Arizona-Nevada. We classified community types, analyzed vegetation-environment relationships, developed ecological species groups (species sharing similar distributions), and evaluated woodland condition. Cluster analysis identified 5 community types at the finest hierarchical level, which were quite distinct floristically (53% mean Sørensen similarity within communities), and included an *A. greggii* community occupying dry washes, 2 *P. glandulosa* communities, a mixed community, and a *P. pubescens* community inhabiting drainage outflows of springs. We recorded a total of 201 taxa. Mean species richness varied significantly among communities from 10 in *P. pubescens* to 35 species/0.1 ha in mixed communities. Environmental variables such as soil texture and cations were related to community gradients, distributions of tree species, and frequency of the tree parasite desert mistletoe (*Phoradendron californicum*). We classified 73 species into 14 species groups, ranging from groups characteristic of uplands (e.g., *Larrea tridentata* group) to those most frequent in lowlands (e.g., *Allenrolfea occidentalis* group). Ecological condition of the woodlands was characterized by well-distributed tree density among size classes (except for *P. pubescens* communities which were dominated by large trees), dominance by native species (94% of total taxa were native), mistletoe infection on 66% of plots, and infrequent evidence of perceived threats (e.g., woodcutting).

RESUMEN

Los bosques de *Acacia greggii*, *Prosopis glandulosa*, y *Prosopis pubescens* tiene prioridad de conservación en el desierto de Mojave por sus valores ambientales. Se midieron la composición de la comunidad vegetal, variables ambientales (ej., gradiente de la ladera, suelo), y condiciones ecológicas (ej., reclutamiento de árboles) en 50 parcelas, de 0.1-ha en las 449,000-ha del Lake Mead National Recreation Area en el este del desierto de Mojave entre Arizona y Nevada. Se clasificaron los tipos de comunidad tipos, se analizaron las relaciones de la vegetación con el ambiente, se desarrollaron grupos ecológicos de especies (especies que comparten distribuciones similares), y se evaluó la condición del bosque. El análisis cluster identificó 5 tipos de comunidad en el nivel jerárquico más fino, que fueron bastante distintos florísticamente (53% de media en el índice de similitud de Sørensen en las comunidades), e incluyó una comunidad de *A. greggii* que ocupa humedales secos, 2 comunidades de *P. glandulosa*, una comunidad mixta, y una comunidad de *P. pubescens* que vive en drenajes de manantiales. se registraron un total de 201 taxa. La riqueza media de especies varió significativamente entre comunidades de 10 en *P. pubescens* a 35 especies/0.1 ha en comunidades mixtas. Las variables ambientales tales como textura del suelo y cationes estaban relacionadas con los gradientes de la comunidad, distribuciones de especies arbóreas, y frecuencia de muérdago parásito de los árboles (*Phoradendron californicum*). Se clasificaron 73 especies en 14 grupos de especies, variando desde grupos característicos de las tierras altas (ej., grupo de *Larrea tridentata*) a los más frecuentes en tierras bajas (ej., grupo de *Allenrolfea occidentalis*). Las condiciones ecológicas de los bosques se caracterizaron por su densidad de árboles bien distribuida entre las clases de tamaño (excepto las comunidades de *P. pubescens* que estaban dominadas por árboles grandes), dominancia de las especies nativas (94% del total de taxa fueron nativos), infección de muérdago en el 66% de las parcelas, y evidencia infrecuente de amenazas percibidas (ej., talas).

INTRODUCTION

Riparian plant communities in the arid American Southwest occupy small portions of landscapes but have disproportionately large habitat value, productivity, and services to humans (Sada et al. 2001; Patten et al. 2008). The valuable functions that riparian ecosystems provide—such as water to sustain human habitations, agriculture, and ranching—and their native biota are threatened by past and present intensive human use of these habitats (Deacon et al. 2007). In the eastern Mojave Desert, for instance, *Acacia greggii*, *Prosopis glandulosa*, and *P. pubescens* riparian woodlands have been destroyed or altered through hydrologic changes and ur-

ban development in Clark County containing metropolitan Las Vegas, Nevada (Crampton & Sedinger 2011). Now covered under a multiple species habitat conservation plan (MSHCP) to forestall U.S. Endangered Species Act listing of associated species, conservation goals for *Acacia* and *Prosopis* woodlands in this region include restoring and maintaining the land area occupied by the woodlands in 2000 (inception of MSHCP), sustaining protected communities in a healthy ecological condition (e.g., well-distributed tree size classes, moderate infection of the tree parasite desert mistletoe [*Phoradendron californicum*], and dominance by native species), and maintaining species affiliated with the woodlands (Crampton et al. 2006).

However, significant knowledge gaps in our understanding of the ecology and conservation needs for these woodlands hinder development of conservation strategies (Crampton et al. 2006). For example, community structure, vegetation-environment relationships, understory composition, and ecological condition of the woodlands including exotic plant invasion status, tree recruitment, desert mistletoe infection, and disturbances such as fire or woodcutting, are poorly understood. Some community classification has been performed in parts of the California Mojave Desert (Evens 2003; Thomas et al. 2004; Keeler-Wolf et al. 2007), but little vegetation-environment research for these communities in the American Southwest has been conducted and conclusions have varied. Some reports in the literature have included that distribution of *Prosopis pubescens* communities was unrelated to gradients in soil pH, soluble salts, or texture along the Rio Grande River in central New Mexico (Campbell and Dick-Peddie 1964). Along the San Pedro River in the Chihuahuan and Sonoran Deserts, *Prosopis velutina* patches occupied sites with low frequency of flooding and highest elevations away from the active flood channel (Bagstad et al. 2006). In Mojave Desert ephemerally moist washes, Evens (2003) noted that *Acacia greggii* occurrences correlated to elevation and amount of topographic protection (concave sites exhibit high protection).

Distinguishing ecological species groups is another means to understand species distributions and vegetation-environment relationships (Goebel et al. 2001). Species groups consist of co-occurring species that share similar environmental affinities and are based on classifying species (rather than communities) into groups usually of 2–10 species displaying similar distributions (Kashian et al. 2003). For example, on a northern Arizona *Pinus ponderosa* forest landscape to the east of the Mojave Desert, we previously classified 18 species groups ranging from plants inhabiting xeric, volcanic cinder soils, to those typifying moist, silt loam soils (Abella & Covington 2006). Species groups are based on a premise that once the groups are developed, presence of some species of a group suggests that environmental characteristics of a site are within the realized niche of the group (Kashian et al. 2003). Ecological species groups have been little developed in southwestern deserts. Species groups have been valuable on other landscapes for understanding vegetation-environment relationships and for management applications such as matching species for ecological restoration to environments where they are best adapted (Goebel et al. 2001).

Exotic plant invasion, tree recruitment, mistletoe infection, and disturbance are additional features related to ecology and condition of *Acacia* and *Prosopis* communities (Stromberg 1993). For example, riparian communities can be highly invadable because of their location along seed dispersal corridors and their resource-rich environment favorable for plant growth (Tabacchi & Planty-Tabacchi 2005). Exotic plant abundance is important to evaluate if dominance by native species is considered a measure of woodland health. Presence of a range of tree size classes is another feature considered desirable for high-quality habitat conditions (Crampton & Sedinger 2011). Tree size and age are not always correlated, but size class analyses are useful for identifying trees that became established more recently than the current largest trees (Miller et al. 2001). Moreover, tree size distribution is important for several other reasons such as suitability of nesting sites for avian species and amount of parasitic mistletoe a tree can support as a food resource for wildlife (Crampton & Sedinger 2011). Mistletoe extracts water and nutrients through a vascular connection to the host tree, with larger trees generally supporting more mistletoe (Watson 2001). Mistletoe is a key food and nesting resource for *Phainopepla nitens*, a conservation-priority bird species covered by the MSHCP, so intermediate amounts of mistletoe are a good indicator of habitat value at a level sustainable to avoid killing trees (Crampton & Sedinger 2011). Disturbances such as fire or woodcutting also can affect ecological condition of woodlands. The wood-

land tree species have some resprouting ability when burned or cut, but these disturbances can reduce their abundance (Stromberg 1993; Busch 1995; Abella 2010).

To help fill knowledge gaps in the ecology of *Acacia* and *Prosopis* woodlands and support development of conservation strategies, we examined plant community structure, vegetation–environment relationships, and ecological condition of these communities on a Mojave Desert landscape of Lake Mead National Recreation Area. Under National Park Service protection, this landscape is viewed as a core conservation area by the MSHCP, which indicates that maintaining quality woodland habitat on this landscape is a key part of conserving these communities in the eastern Mojave Desert (Crampton et al. 2006). Specific study objectives were to: (1) develop a hierarchical classification and identify diagnostic species for *Acacia* and *Prosopis* woodlands; (2) identify vegetation–environment relationships of communities and distributions of tree species; (3) develop ecological species groups; (4) examine species richness relationships with community types, environmental gradients, and exotic species; and (5) assess current woodland condition, including tree recruitment, mistletoe infection, and evidence of disturbances such as fire or woodcutting.

METHODS

Study Area

We conducted this study in Lake Mead National Recreation Area, a 449,000-ha unit (excluding full-pool areas of Lakes Mead and Mohave) of the National Park Service, in southeastern Nevada and northwestern Arizona in the eastern Mojave Desert (35°59'N, 114°51'W; Fig. 1). The centrally located Boulder City, Nevada, weather station has reported the following averages: 14 cm/yr of precipitation, 4°C January daily low temperature, and 39°C July high temperature (768 m elevation, 1937–2004 records; Western Regional Climate Center, Reno, Nevada). Consistent with the Mojave Desert's status as a winter rainfall desert (Keeler-Wolf et al. 2007), 70% of precipitation falls from September through April. Predominant landforms include low mountain ranges, bajadas (coalesced alluvial fans), relatively flat plains, washes serving as intermittent drainageways, and playas (dry lakes). Mapped soil types include Aridisol and Entisol orders (Lato 2006). Uplands, which occupy >90% of the area, are dominated by shrublands of *Larrea tridentata* and *Ambrosia dumosa* (Abella et al. 2012a). Communities containing *Acacia* or *Prosopis* are associated with washes, springs, and topographically protected sites (Fig. 2). Major large herbivores include exotic *Equus asinus* in some areas and native *Ovis canadensis* and smaller animals such as *Lepus californicus*. Some unauthorized cattle grazing occurs in the northeastern part of the study area. Human recreation use is concentrated along access points of Lake Mead's shoreline and Colorado River south of Hoover Dam and along major roads (Fig. 1).

DATA COLLECTION

We used an existing map of *Acacia greggii*, *Prosopis glandulosa*, and *Prosopis pubescens* distribution within the study area (Crampton et al. 2006), combined with our own field reconnaissance, to identify 118 polygons ≥ 0.25 ha and containing $\geq 2\%$ cover of one or more of these species. This cover criterion excluded sampling sites containing only an individual tree. We randomly selected 50 of these polygons for sampling, ranging in size from 0.25–89 ha. We generated a random Universal Transverse Mercator (UTM) coordinate using a geographic information system (ArcMap, Esri Corporation, Redlands, California) within each polygon (subdivided by tree species) at which to establish a plot. Plots were 0.1 ha and were 20 m \times 50 m (45 of the 50 plots) where the landform allowed; otherwise 33.3 m \times 33.3 m (5 plots). We sampled plots from July–October 2011, during the leaf-on period for the deciduous *Acacia* and *Prosopis*.

We measured the plant community on each plot by visually categorizing areal cover of vascular plant species using cover classes: trace (assigned 0.2% for analyses), < 1% (assigned 0.5%), 1% intervals to 5%, and thereafter 5% intervals. The same botanist measured all plots for consistency in cover categorization. Along with live plants, standing dead annual plants, noted to persist for 1–2 years in the Mojave Desert (Beatley 1966), were included in sampling to more thoroughly characterize the annual plant community. Plants not identifiable in the field were collected, pressed, and keyed to the finest taxonomic level possible. Four speci-

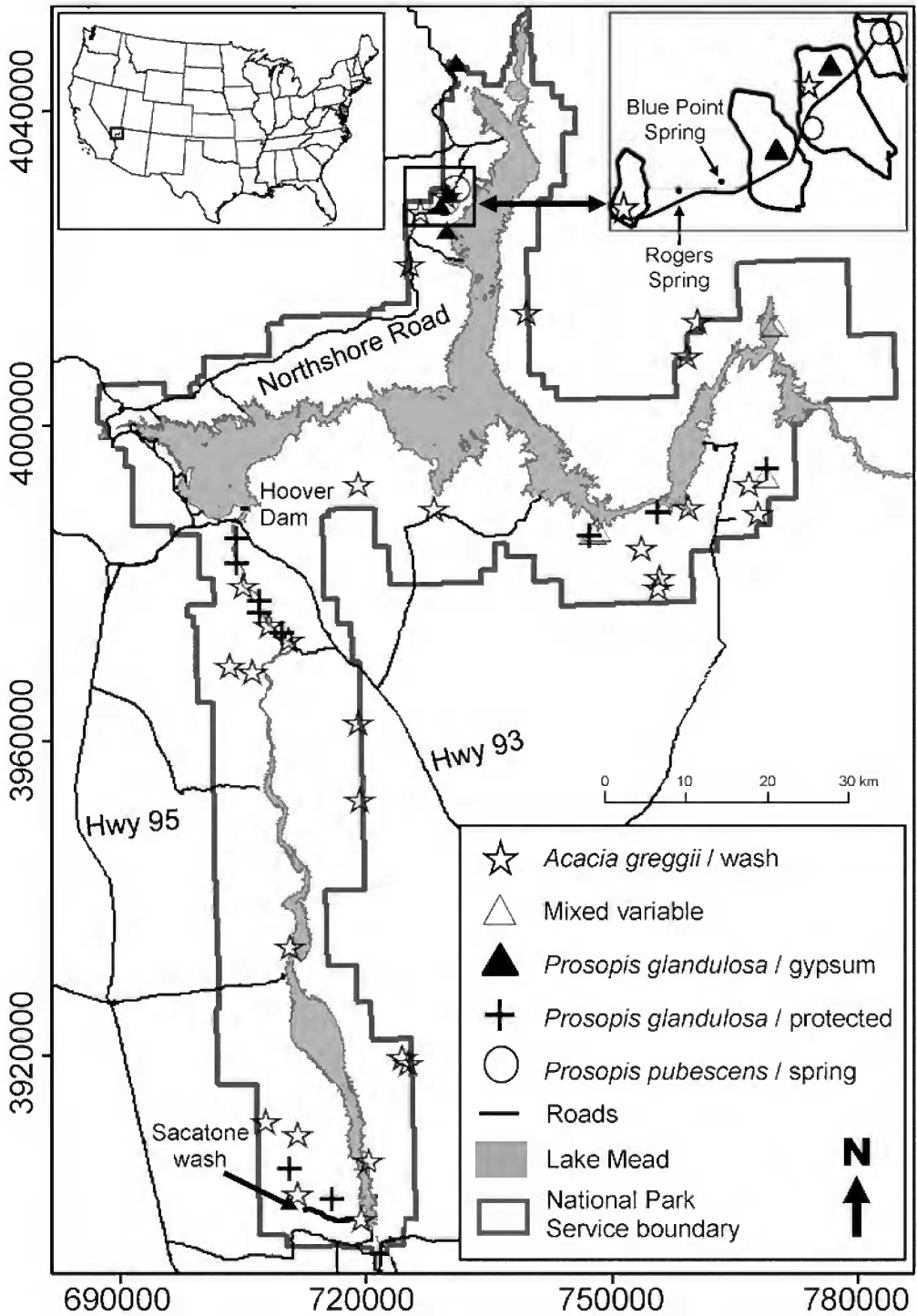


FIG. 1. Distribution of 50 sample plots displayed by community type and locations mentioned in the text for *Acacia* and *Prosopis* woodlands of the eastern Mojave Desert, USA. The inset at the top right includes mapped polygons of the tree species with randomly located plots within. Coordinates are Universal Transverse Mercator (m), North American Datum 1983.

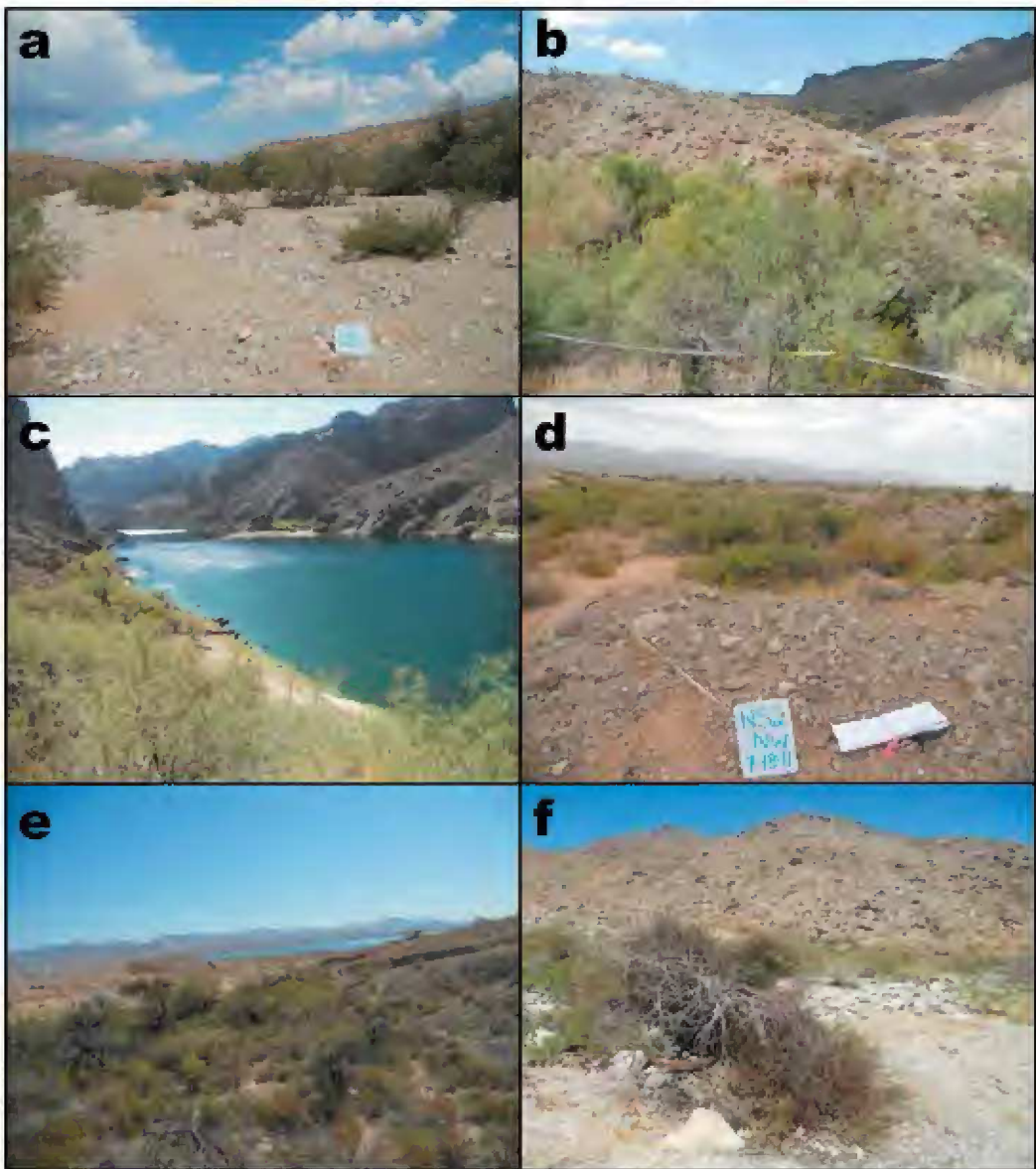


FIG. 2. Examples of woodland community types of the eastern Mojave Desert, USA: (a) *Acacia greggii*/wash, (b) Mixed/variable, (c) *Prosopis glandulosa*/protected, (d) *Prosopis glandulosa*/gypsum, and (e) *Prosopis pubescens*/spring. Desert mistletoe is shown in the foreground of (f) parasitizing an *Acacia greggii* tree.

mens out of 1385 total plant records across plots were not identifiable to at least family and were deleted from the data set. Classification of taxa to growth form (forb, shrub, or tree), life span (e.g., annual), and native/exotic status to North America followed USDA, NRCS (2012).

Live and dead individuals (of all sizes including seedlings) for all tree species were counted on each plot and their height was determined using a measuring pole. We measured diameter at root collar for the largest stem for all individuals and diameter at breast height (137 cm) for each tree taller than breast height. To measure mistletoe infection on each tree, we used the Hawksworth (1977) 6-class mistletoe rating. Infection was

recorded as none (assigned 0), light ($\leq 50\%$ of branches infected, assigned 1), or heavy ($> 50\%$ of branches infected, assigned 2) for each third of the tree. The values were summed to result in a 0 (no infection) to 6 (heavy) rating (Hawksworth 1977).

Data regarding depth to groundwater and ground-water chemistry would be desirable. These data were not available for the study area (Gary Karst, Hydrologist, Lake Mead National Recreation Area, pers. comm.) and were difficult or not permissible to obtain through drilling monitoring wells. We were able, however, to collect a variety of environmental data for each plot including location, topography, disturbance, and soil. We recorded elevation and location (UTM, using a global positioning system, at the southwestern plot corner), slope gradient (clinometer), aspect (compass), and landform type (e.g., wash; following Lato [2006]). In addition to capturing possible variation unaccounted for by other environmental variables, location can represent influences such as historical disturbance difficult to detect but potentially influencing site-specific vegetation patterns. We linearized aspect to range from 0 (southwest) to 2 (northeast; Beers et al. [1966]). We obtained 1971–2000 mean annual precipitation and temperature for each plot location from PRISM (Daly et al. 2008). We qualitatively noted visual evidence of disturbance, such as fire, off-road vehicle tracks, woodcutting, and livestock presence (animals or dung).

We collected 3 subsamples of the 0–5 cm mineral soil from each of 3 different interspaces ≥ 1 m from the outermost edge of a tree canopy. To measure bulk density, we collected a sample of approximately 400 cm³ from the same interspaces. Soil samples were composited by plot. We sieved air-dried analytical samples to pass a 2-mm sieve and analyzed the fine fraction for texture (hydrometer method) following Tan (2005); pH and electrical conductivity (1:1 soil:water); available P (Olsen sodium-bicarbonate extraction); CaCO₃ (manometer method); total C, N, and S (dry combustion, CNS analyzer); organic C (difference between total and inorganic C); NO₃, SO₄, and Cl (ion chromatography); and the water-soluble concentrations of Na, K, Mg, Ca, Mn, Fe, Ni, Cu, Zn, Co, B, Mo, Pb, and Cd (1:3 soil:water extracts, inductively coupled plasma mass spectroscopy) following Burt (2004). We estimated bulk density by sieving through a 2-mm sieve, oven drying the < 2 -mm fraction at 105°C for 24 h, and including volume of coarse fragments > 2 mm in the total soil volume. We used bulk density to convert nutrient concentrations to volumetric contents (Burt 2004). Because concentrations and contents were strongly correlated (e.g., $r = 0.95$ for organic C, 0.92 for total N, and 1.00 for total S), we report concentrations.

DATA ANALYSIS

We conducted multivariate plant community and soil analyses using version 6.07 of PC-ORD software (McCune and Mefford 1999). We used hierarchical cluster analysis (Sørensen index and flexible beta [$\beta = -0.25$] linkage method) to classify plots by species composition based on relative cover (cover of species_{*i*}/cover of all species on a plot). To identify species with the greatest fidelity to each hierarchical plot grouping, we used indicator species analysis to produce an indicator value ranging from 0 (no fidelity) to 100% (highest fidelity) based on relative cover and relative frequency among the groups (Dufrêne & Legendre 1997). We ordinated species composition (relative cover) with non-metric multi-dimensional scaling through PC-ORD's autopilot, slow and thorough routine. Environmental variables and species displaying the strongest correlations with community compositional patterns were displayed as vectors scaled to the strength and direction of correlations. We ordinated soil composition using principal components analysis, with the cross-products matrix derived from correlation to account for different measurement scales of soil variables.

We used SAS 9.2 software (SAS Institute 2009) to conduct univariate and bivariate analyses. We used a Kruskal-Wallis test followed by Tukey's test on ranks for multiple comparisons to compare species richness among plant community types at the finest level of the cluster analysis community classification. We used Pearson correlation to assess the relationship of native and exotic species richness.

To identify biophysical correlates with distribution of community types, tree species, and measures of ecological condition (exotic species richness and cover, tree recruitment, and mistletoe), we used classification (for categorical response variables) and regression trees (for continuous response variables) in JMP 9 software (SAS Institute 2010). Regression trees are nonparametric models that partition data into increasingly homog-

enous subsets and provide dichotomous keys to estimate a dependent variable at different levels of explanatory variables (Breiman et al. 1984). Dependent variables were screened for inclusion in models based on a criterion of minimizing total sums of squares at different splits. Splitting stopped when adding more explanatory variables increased r^2 by <0.05 or when the minimum node size ($n = 5$ for most analyses) was reached. There is essentially no limit to the number of independent variables that can be input to each model because a screening process identifies variables with the strongest explanatory power for inclusion in final models (SAS Institute 2010). We employed JMP's k -fold crossvalidation ($k = 3$ or 5) to compute a cross-validated r^2 . We explored modelling several tree recruitment (e.g., trees/ha or percent of total trees by height and diameter at root collar and breast height classes) and mistletoe (e.g., proportion of infected trees, infected trees/ha, total Hawksworth rating) measures. The final model for recruitment portrayed percent of trees in the 1–9 cm root collar diameter class, because root collar differentiated trees with large stems that might be short in height yet still old (Miller et al. 2001) and the model displayed the highest r^2 among recruitment measures. We chose the final mistletoe model to portray infected trees/ha because Crampton and Sedinger (2011) found that this measure was correlated to *Phainopepla nitens* nesting preference and this response variable also yielded the highest model r^2 in our study.

We constructed ecological species groups by: (1) including only species occupying ≥ 3 plots; (2) relativizing species cover by species sums of squares to emphasize habitat preferences, avoiding groupings based on the commonness or rarity of species (McCune et al. 2000); and (3) grouping species through cluster analysis (Sørensen distance and -0.25 Flexible Beta group linkage) in PC-ORD (McCune & Mefford 1999). We used Pearson correlation to relate average cover of species groups to principal components and environmental variables.

RESULTS

Community Classification

At the coarsest grouping, cluster analysis classified plots into an *Acacia greggii*-dominated group and those containing *Prosopis* spp. (Fig. 3). Finer groupings distinguished *Prosopis pubescens*, two types of *Prosopis glandulosa* communities, and a mixed community of *A. greggii*, *Prosopis* spp., and other species. Sørensen similarity among plots within a community at the finest level ranged from 42% (*Acacia greggii*/wash) to 66% (*Prosopis glandulosa*/protected) and averaged $53 \pm 10\%$ (\pm SD, $n = 5$ community types). We named the 5 community types at the finest hierarchical level according to dominant tree species and either a commonly associated topographic feature or soil parent material (Table 1).

There were significant indicator species at each level of the community hierarchy. At the finest level, understory species such as *Hymenoclea salsola* were significantly associated with the *Acacia greggii*/wash community; cacti species and *Baccharis salicifolia* with Mixed/variable; *Isocoma acradenia*, *Atriplex confertifolia*, and *Suaeda moquinii* with *Prosopis glandulosa*/gypsum; and *Allenrolfea occidentalis* and *Distichlis spicata* with *Prosopis pubescens*/spring. Cluster analysis combined with indicator species analysis suggested that the vegetation was readily distinguishable into community types at multiple hierarchical levels.

Species Richness

A total of 201 taxa (90% identified to species) were detected on plots. This flora consisted of 61 annual forb (30%), 47 shrub (23%), 41 perennial forb (20%), 14 annual-perennial forb (7%), 9 cactus (4%), 9 perennial graminoid (4%), 7 tree (3%), 6 annual grass (3%), 5 annual-biennial forb (2.5%), 1 annual-perennial grass (0.5%), and 1 perennial fern (0.5%). Species richness varied significantly (Kruskal-Wallis $\chi^2 = 18.4$; $P = 0.001$) among communities from 10 (*Prosopis pubescens*/spring) to 35 species/0.1 ha (Mixed/variable; Fig. 4A). Even including dead annual plants, richness in all communities was dominated by perennials.

Vegetation and Soil Gradients

The vegetation ordination corroborated cluster analysis with distinct community groupings evident in the ordination (Fig. 5A). Whereas *Acacia greggii*-dominated plots clearly separated from those of other communities, plots within this community displayed a large spread consistent with their low similarity (42%) in cluster analysis. *Acacia greggii* plots in the lower part of the ordination grouping had the greatest relative cover of *Aca-*

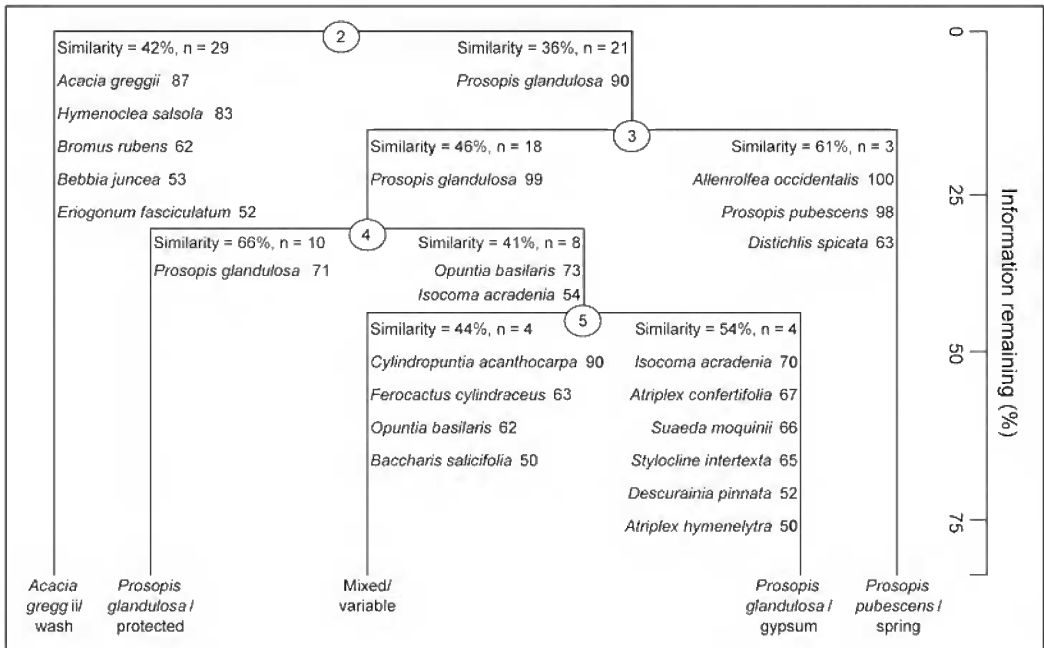


Fig. 3. Hierarchical community classification of *Acacia* and *Prosopis* woodlands of the eastern Mojave Desert, USA. Internal Sørensen similarity, number of plots, and indicator species and indicator values significant at $P < 0.05$ and ≥ 50 are shown at each division. Community types at the finest level of the classification are named according to dominant tree species and environmental features.

cia, whereas plots in the upper part exhibited greater relative cover of species such as *Ambrosia dumosa*, *Hymenoclea salsola*, and *Eriogonum fasciculatum*. Some environmental variables were correlated with vegetation gradients. Coarse-textured soil, for example, was associated with *A. greggii* communities, and total S and several cations correlated with *Prosopis glandulosa*/gypsum communities.

In contrast to vegetation that clearly grouped into community types, ordination of soil properties did not display strong grouping (Fig. 5B). Some plots, associated with gypsum, were correlated with soil electrical conductivity, SO_4 , and various elements along axis 1. Axis 2 displayed few relationships.

Whereas multivariate variation in soil properties was not strongly linked to plant community gradients, examining means in individual soil properties suggested several findings (Table 2). Variability across communities differed among properties, with some properties (e.g., B) displaying extreme variation in orders of magnitude. Certain properties, such as total S, were highly variable within communities (e.g., 398% coefficient of variation for S in *Acacia greggii*/wash), yet some of these properties like S were still orders of magnitude greater in one or more communities. A community could occupy a range of values in soil properties, but there were some properties exhibiting especially large or small values in particular communities.

Community and Tree Species Distribution

Effectiveness of classification or regression tree models and variables they included differed for portraying distributions of communities and tree species (Fig. 6). A classification tree selected UTM coordinates and sand concentration as most important for differentiating communities. High sand concentration was again related to *Acacia greggii*/wash communities, as in the ordination. The UTM coordinates corresponded with distribution of soil parent materials, such as gypsum, which occupied the northeastern part of the study area, and topographic features like Black Canyon (below the Hoover Dam; Fig. 1). A classification tree of *Prosopis pubescens* with gypsum). A regression tree for *A. greggii* canopy cover illustrated that soil of low electrical conductivity

TABLE 1. Characteristics of *Acacia* and *Prosopis* woodland community types of Lake Mead National Recreation Area, Mojave Desert, USA.

| | <i>Acacia greggii</i> / wash | Mixed/ variable | <i>Prosopis glandulosa</i> / protected | <i>Prosopis glandulosa</i> / gypsum | <i>Prosopis pubescens</i> / spring |
|--------------------------------------|---------------------------------|-------------------------------|---|--|---------------------------------------|
| Number of plots | 29 | 4 | 10 | 4 | 3 |
| Live trees/ha (mean±SD) | 230±126 | 330±88 | 239±79 | 508±319 | 197±124 |
| Live trees/ha (range) | 50–600 | 200–390 | 120–370 | 170–910 | 120–340 |
| <i>Acacia greggii</i> (%) | 99 | 39 | 44 | 0 | 0 |
| <i>Prosopis glandulosa</i> (%) | 1 | 59 | 56 | 100 | 0 |
| <i>Prosopis pubescens</i> (%) | 0 | 2 | 0 | 0 | 100 |
| Live trees infected (%, mean±SD) | 19±23 | 16±15 | 19±16 | 11±13 | 50±25 |
| Live trees infected (%, range) | 0–86 | 0–35 | 0–48 | 2–29 | 21–67 |
| Elevation (m, mean±SD) | 581±255 | 457±93 | 370±170 | 424±47 | 460±9 |
| Elevation (m, range) | 201–1154 | 381–590 | 198–685 | 379–469 | 455–471 |
| Slope gradient (%, mean±SD) | 4±6 | 10±6 | 17±19 | 3±11 | 6±3 |
| Slope gradient (%, range) | 1–31 | 3–18 | 2–52 | 2–4 | 3–9 |
| Topography | Washes | Variable | Canyons, concave | Washes, depressions | Spring drainages |
| Soil classification (great group) | Torriorthents Haplocalcids | Torriorthents Haplocalcids | Torriorthents | Haplogypsisds Haplocalcids | Petrogypsisds Haplogypsisds |

had the greatest canopy cover. On soil with higher conductivity, the greatest *A. greggii* canopy cover occurred on soil with low SO_4 and high gravel concentration. Canopy cover of *Prosopis glandulosa* exhibited a different pattern: it was greatest on soil rich in NO_3 , or on sites with steep slopes when soil NO_3 was low.

Ecological Condition and Species Groups

Thirteen exotic species were detected, including the annual grasses *Bromus rubens* (86% of plots), *Schismus* spp. (76%), *Polypogon monspeliensis* (10%) and *Bromus tectorum* (8%); annual forbs *Brassica tournefortii* (6%), *Salsola tragus* (6%), *Malcolmia africana* (4%), and *Sonchus asper* (2%); annual-biennial forbs *Erodium cicutarium* (28%), *Lactuca serriola* (2%), and *Sisymbrium altissimum* (2%); the perennial forb *Marrubium vulgare* (2%); and the tree *Tamarix ramosissima* (22%). *Prosopis pubescens*/spring contained no plots with exotic species, and average exotic richness ranged from 2–4 species/0.1 ha in the other communities. Native and exotic species richness were positively related ($r = 0.47$; Fig. 4B). This correlation was larger than the next highest correlations that exotic richness exhibited ($r = 0.35$ with precipitation and 0.34 with UTMx).

A regression tree portraying exotic species richness accounted for 40% of variance upon crossvalidation (Fig. 7A), which was higher than the 17% for exotic cover (not shown). The regression tree indicated that sites with ≥ 16 cm/yr of precipitation and silty soil contained the most exotic species. The least exotic rich were drier sites, especially those with high soil S.

Mistletoe was present on 33 of 50 plots (66%), and the percentage of trees infected was 50% in the *Prosopis pubescens*/spring community and lower (11–19%) in other communities (Table 1). The greatest density of infected trees portrayed by a regression tree occurred on soil with low CaCO_3 concentration, or, if CaCO_3 concentration was high, on higher elevation sites with high tree canopy cover (Fig. 7B).

Tree size-class distributions revealed that densities were variable within diameter classes among sites within communities (Fig. 8). This resulted from some sites containing few or no trees in some size classes. Communities as a whole exhibited good representation of small trees, with generally as many or more trees in small as large size classes. The exception was the *Prosopis pubescens*/spring community, which mostly contained large trees. Density of trees in the smallest size class (1–9 cm diameter at root collar) was positively correlated with total tree density ($r = 0.73$). A regression tree showed that the greatest percentage of small trees occurred on sites with high precipitation and in areas other than the northeastern part of the study area (Fig.

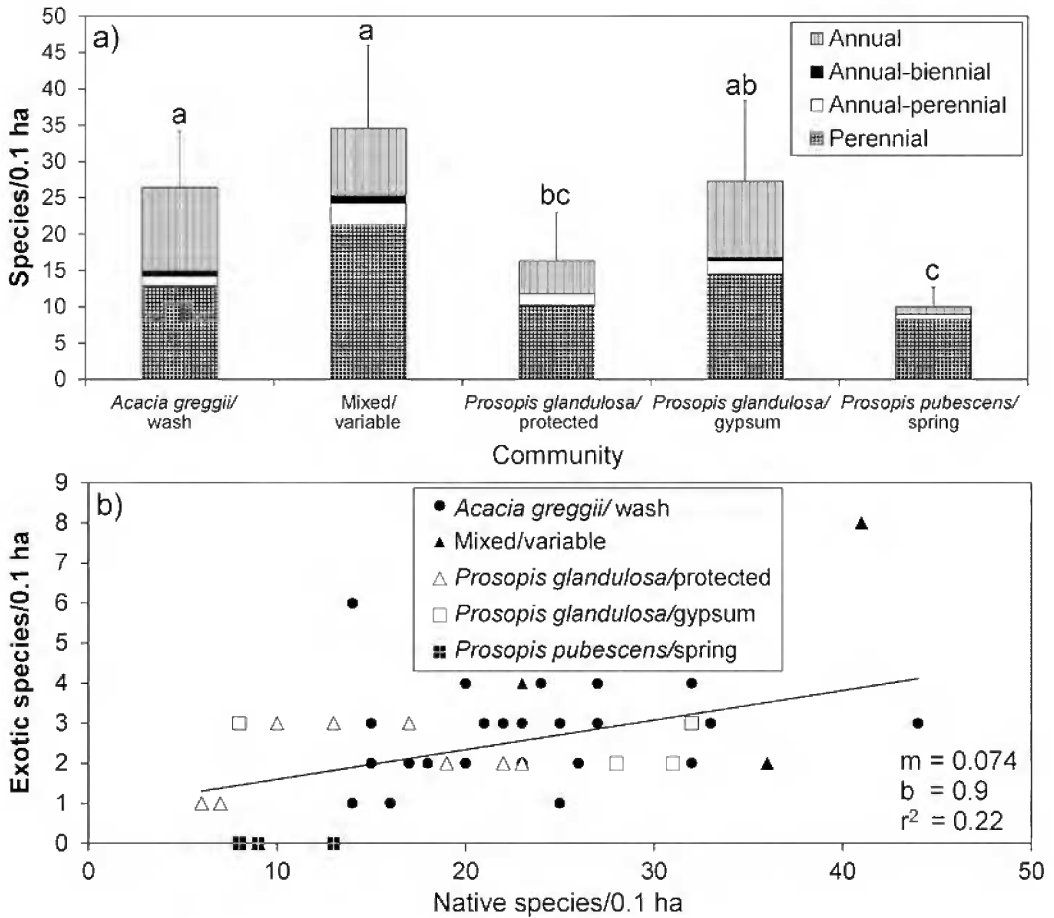


FIG. 4. (a) Species richness by lifeform for *Acacia* and *Prosopis* woodlands of the eastern Mojave Desert, USA. Error bars are 1 SD for total mean richness, and means without shared letters differ at $P < 0.05$. (b) Relationship between native and exotic species richness, with a slope and y intercept for a regression line shown for descriptive purposes.

7C). *Prosopis pubescens*/spring communities, which were dominated by large trees, occurred in the study area's northeastern corner.

We classified a total of 73 species into 14 species groups comprised of 2–8 species (Appendix 1). Amplitude and fidelity to community types varied among species groups, with some groups most frequent in one or a few communities (e.g., *Allenrolfea occidentalis* group most frequent in *Prosopis pubescens*/spring) and others more widespread yet still often sparse or absent from one or more communities. Examples of species group distributions include: the *Acacia greggii* group of *Hymenoclea salsola* and annual species like *Eriogonum palmelianum* that occupy washes; *Larrea tridentata* group of dry-site species inhabiting xeric areas within or on the edges of the sampled riparian patches; *Encelia farinosa* group of *Acacia greggii*/wash but also of other communities, excepting *Prosopis pubescens*/spring; *Pluchea sericea* group with a distribution difficult to characterize; *Suaeda moquinii* principally of gypsum soil, including *Prosopis glandulosa*/gypsum and *Prosopis pubescens*/spring, although some species of the group also frequented other communities; and the *Allenrolfea occidentalis* group primarily of *Prosopis pubescens*/spring or *Prosopis glandulosa*/gypsum, indicating that this group inhabits extreme soil properties. Exotic species did not group together (only one species group contained more than one exotic species) and instead occurred in a range of species groups with native species.

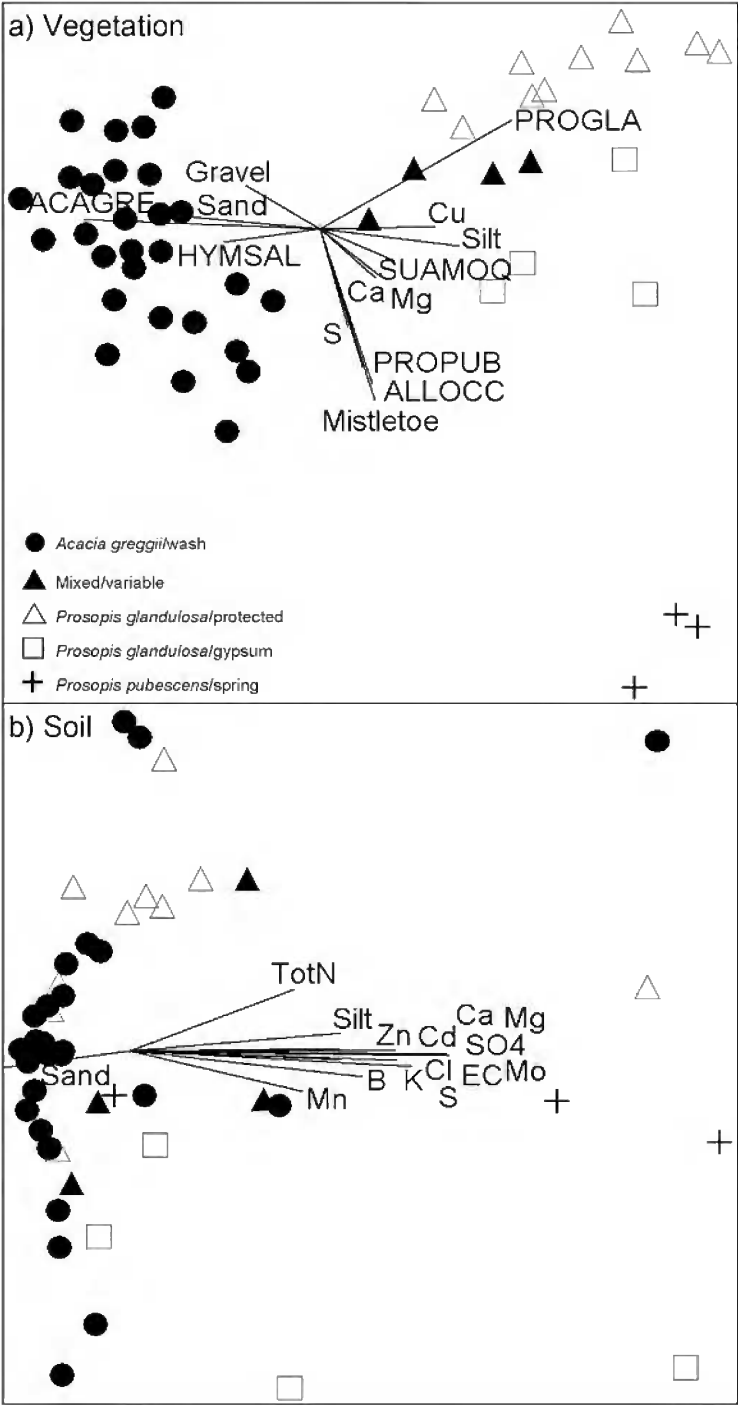


FIG. 5. Ordination of (a) vegetation and (b) soil composition with plots displayed according to community type for *Acacia* and *Prosopis* woodlands of the eastern Mojave Desert, USA. Vectors are scaled in proportion to their correlation with ordination axes. Vectors are shown with $r^2 \geq 0.20$ for (a) and ≥ 0.50 for (b). Abbreviations for vectors: ACAGRE = *Acacia greggii*, ALLOCC = *Allenrolfea occidentalis*, HYMSAL = *Hymenoclea salsola*, PROGLA = *Prosopis glandulosa*, PROPUB = *Prosopis pubescens*, and SUAMOQ = *Suaeda moquinii*.

TABLE 2. Soil properties (0–5 cm) of *Acacia* and *Prosopis* woodland community types of Lake Mead National Recreation Area, Mojave Desert, USA.

| | AG/wash ^a | M/variable | PG/protected | PG/gypsum | PP/spring |
|-----------------------------------|----------------------|------------|--------------|-----------|-------------|
| Physical properties | Mean ± SD | | | | |
| Gravel (% weight) | 46±14 | 37±17 | 43±17 | 21±21 | 3±3 |
| Gravel (% volume) | 28±10 | 19±17 | 24±11 | 13±15 | 1±1 |
| Bulk density (g/cm ³) | 0.78±0.23 | 0.83±0.2 | 0.70±0.13 | 0.93±0.1 | 0.67±0.06 |
| Sand (%) | 86±13 | 72±7 | 72±16 | 75±18 | 53±22 |
| Silt (%) | 8±9 | 22±7 | 20±13 | 14±7 | 40±19 |
| Clay (%) | 6±4 | 7±2 | 9±4 | 11±11 | 7±4 |
| Chemistry | | | | | |
| EC ^b (mS/cm) | 2.5±11.0 | 2±2.3 | 3.3±8 | 9.5±10.9 | 16.9±14.2 |
| pH | 8.0±0.3 | 8±0.5 | 7.7±0.3 | 8±0.6 | 8.4±0.3 |
| Chemical composition | | | | | |
| CaCO ₃ (%) | 9.1±15.6 | 13.6±5.1 | 7.4±7.0 | 26.1±12.0 | 2.7±0.6 |
| Organic C (%) | 0.6±0.8 | 0.7±0.6 | 0.7±0.5 | 0.7±0.5 | 1.1±0.6 |
| Inorganic C (%) | 1.1±1.9 | 1.6±0.6 | 0.9±0.8 | 3.1±1.4 | 0.3±0.1 |
| Total C (%) | 1.6±2.1 | 2.3±1.0 | 1.5±0.8 | 3.8±1.1 | 1.4±0.5 |
| NO ₃ (mg/kg) | 0.7±0.6 | 4.9±8.5 | 6±7.6 | 18.6±36.3 | 5.1±7.6 |
| Total N (%) | 0.04±0.04 | 0.08±0.06 | 0.06±0.04 | 0.07±0.07 | 0.10±0.05 |
| Olsen P (µg/g) | 6±5 | 15±15 | 9±7 | 19±18 | 13±11 |
| SO ₄ (mg/kg) | 400±1924 | 253±417 | 533±1593 | 627±611 | 2243±1935 |
| Total S (%) | 0.20±0.81 | 0.12±0.13 | 0.15±0.36 | 0.07±0.04 | 3.39±2.92 |
| K (mg/kg) | 235±834 | 181±178 | 142±152 | 376±259 | 470±336 |
| Ca (mg/kg) | 523±1142 | 1008±1416 | 543±864 | 2498±1506 | 2870±2218 |
| Mg (mg/kg) | 81±196 | 173±210 | 105±195 | 314±258 | 497±384 |
| Na (mg/kg) | 449±1586 | 466±532 | 302±525 | 752±761 | 1230±846 |
| Fe (µg/kg) | 114±144 | 55±45 | 119±103 | 57±31 | 100±41 |
| Mn (µg/kg) | 0.03±0.04 | 0.05±0.02 | 0.03±0.03 | 0.12±0.09 | 0.09±0.02 |
| Cu (µg/kg) | 33±25 | 53±20 | 82±60 | 59±23 | 69±25 |
| Zn (µg/kg) | 18±44 | 15±18 | 46±77 | 24±18 | 69±53 |
| Mo (µg/kg) | 3.8±17.8 | 2.5±3.2 | 3±7.2 | 3±3 | 13.7±12.7 |
| B (µg/kg) | 657±2537 | 629±803 | 1094±2964 | 2953±4712 | 19469±24806 |
| Cl (mg/kg) | 251±1314 | 138±250 | 148±402 | 856±1256 | 1264±1130 |
| Ni (µg/kg) | 11±8 | 17±7 | 10±7 | 16±12 | 12±10 |
| Co (µg/kg) | 0.7±1.0 | 1.3±1.3 | 1.5±1.6 | 1.8±2 | 1.1±0.6 |
| Cd (µg/kg) | 0.09±0.33 | 0.06±0.04 | 0.09±0.15 | 0.11±0.06 | 0.25±0.24 |
| Pb (µg/kg) | 0.4±0.4 | 0.2±0.1 | 0.6±0.4 | 0.2±0.1 | 0.4±0.2 |

^a From left to right, full names of community types are: *Acacia greggii*/wash, Mixed/variable, *Prosopis glandulosa*/protected, *Prosopis glandulosa*/gypsum, and *Prosopis pubescens*/spring
^b Electrical conductivity

Nine of the 14 species groups had correlation coefficients $\geq |0.40|$ with at least one principal component or environmental variable. Among the strongest correlations included the *Acacia greggii* group with precipitation ($r = 0.55$), sand ($r = 0.60$), and total N ($r = -0.46$); *Pluchea sericea* group with Cu ($r = 0.72$); and the *Allenrolfea occidentalis* group with total S ($r = 0.64$).

DISCUSSION

Community Classification and Gradients

Plant species composition was distinct for each community type, and distributional overlap among the three tree species was low at our 0.1-ha plot scale. With an internal similarity of 44%, even the mixed/variable community was not merely a collection of sites unable to be classified, but rather was a community of unique species composition. Uniqueness of community composition was illustrated by internal similarities of 42–66% and segregation of community groupings in ordination. Only 1 (2%) of 50 plots contained all three focal tree species and 10 (20%) contained two species (all co-occurrences of *Acacia greggii* and *Prosopis glandulosa*), suggesting relatively strong partitioning of species distributions. Based on soil texture and landforms, we surmise

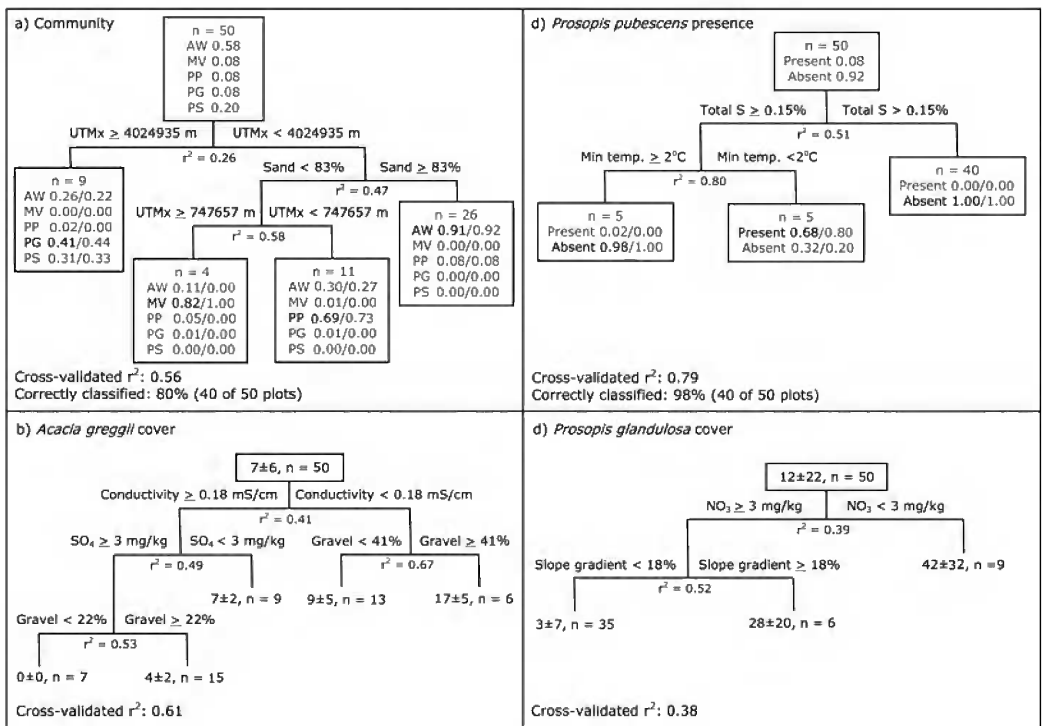


Fig. 6. Distribution of community types and tree species as a function of environmental variables for *Acacia* and *Prosopis* woodlands of the eastern Mojave Desert, USA. (a) Classification tree for distribution of community types, abbreviated as: AW = *Acacia greggii*/wash, MV = Mixed/variable, PP = *Prosopis glandulosa*/protected, PG = *Prosopis glandulosa*/gypsum, and PS = *Prosopis pubescens*/spring. The actual proportion of plots is shown at the top of the tree. For each division, the estimated probability is shown on the left and the actual proportion on the right, with bold font highlighting the community with the highest estimated probability. (b) Regression tree with estimated mean (\pm SD) *Acacia* canopy cover at terminal nodes. (c) Classification tree of *Prosopis pubescens* presence/absence, with estimated probability of presence shown on the left and actual proportion of presence on the right for each division. (d) Regression tree with estimated mean (\pm SD) *Prosopis glandulosa* canopy cover at terminal nodes.

that *A. greggii* generally occupied the driest sites (coarsest soil and dry washes), *P. glandulosa* intermediate (topographically protected and moister washes), and *Prosopis pubescens* the wettest (outflow of springs, often with visible surface water). Comparative ecohydrological research (Smith et al. 1998) may be useful for evaluating if water balances were consistent with this perceived distribution.

Ordinations suggested that vegetation grouped more strongly than did the suite of 31 measured soil variables and that plant communities inhabited a range of environmental properties. However, there were some environmental correlates for the communities and tree species. Coarse-textured soil was associated with *Acacia greggii*, reflecting this species' affinity for dry washes. These washes have coarse soil because periodic floods carry away fine soil particles, while depositing coarse material from higher elevations (Schwinning et al. 2011). UTM, expressing location, was also an important variable, suggesting that certain communities had affinity to particular sections of the study area. *Prosopis pubescens*/spring communities, for example, were located in the northeastern part of the study area where hydrological conditions associated with outflow of springs were apparently favorable for development of this community. These areas were also affiliated with gypsum soil, likely accounting for relationships of *Prosopis pubescens*/spring communities with variables such as total S. Gypsum, comprised of $CaSO_4 \cdot 2H_2O$, produces soils high in S and salts (Meyer 1986) and can have extreme properties compared to the rest of the landscape, as we observed in our study. *Prosopis pubescens* occupies non-gypsum soil in other parts of its range (Busch 1995), and it is unclear if *P. pubescens* simply is toler-

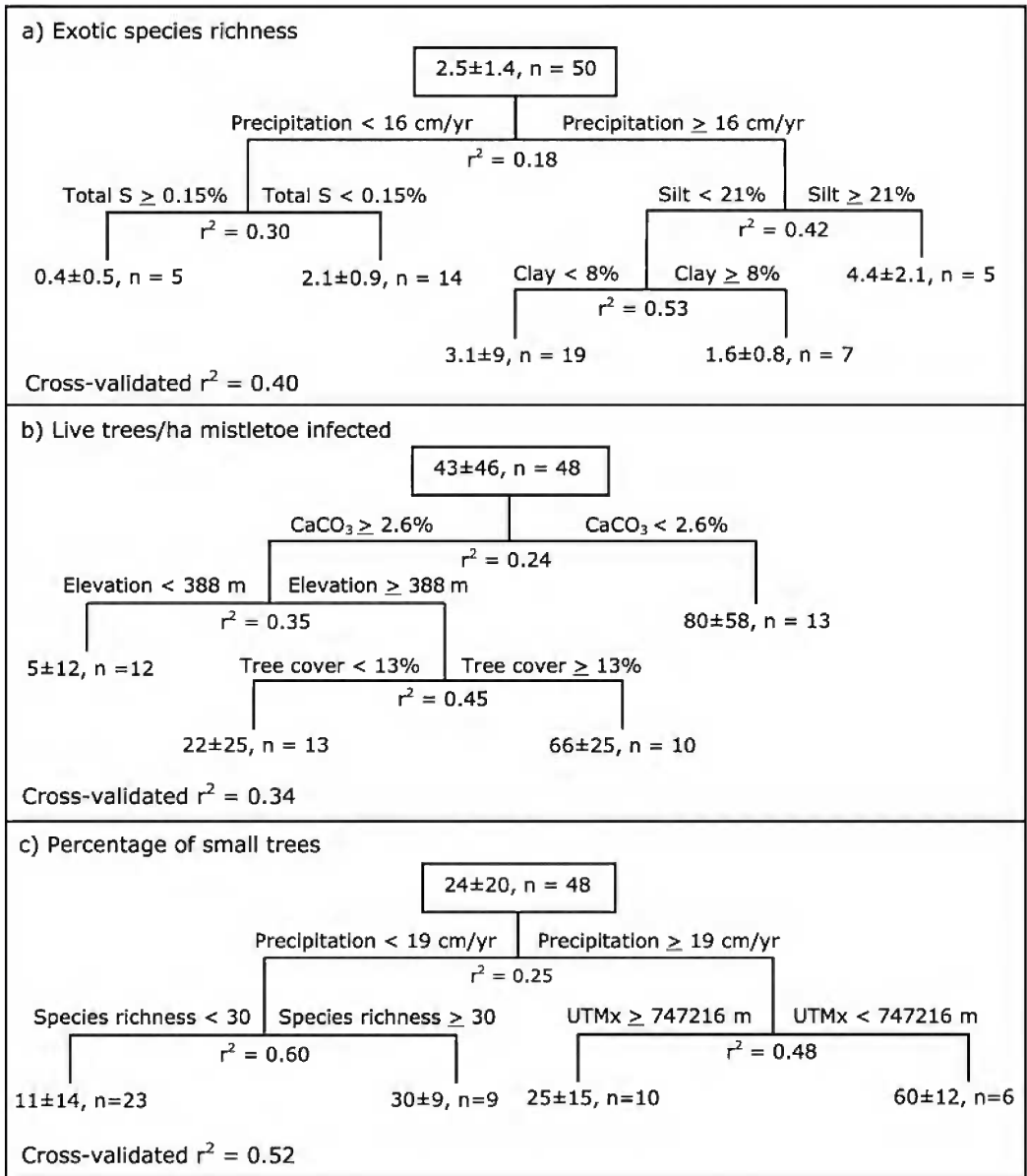


FIG. 7. Regression trees for ecological condition variables of *Acacia* and *Prosopis* woodlands of the eastern Mojave Desert, USA. Cumulative r^2 is shown for each division and estimated means (\pm SD) of response variables at terminal nodes. Trees could not be counted due to inaccessibility at 2 plots so sample size is 48 for (b) and (c).

ant of the extreme properties of gypsum in our study or if environmental conditions favorable for its occurrence were related to gypsum soil properties.

Although potential importance of plant correlations with soil variables should not be dismissed, data on ground-water depth and chemistry might help to account for additional variance in community and tree species distribution. Few data on groundwater exist for the study area (Gary Karst, Hydrologist, Lake Mead National Recreation Area, pers. comm.). An unpublished report using six wells found that depth to groundwater was <1

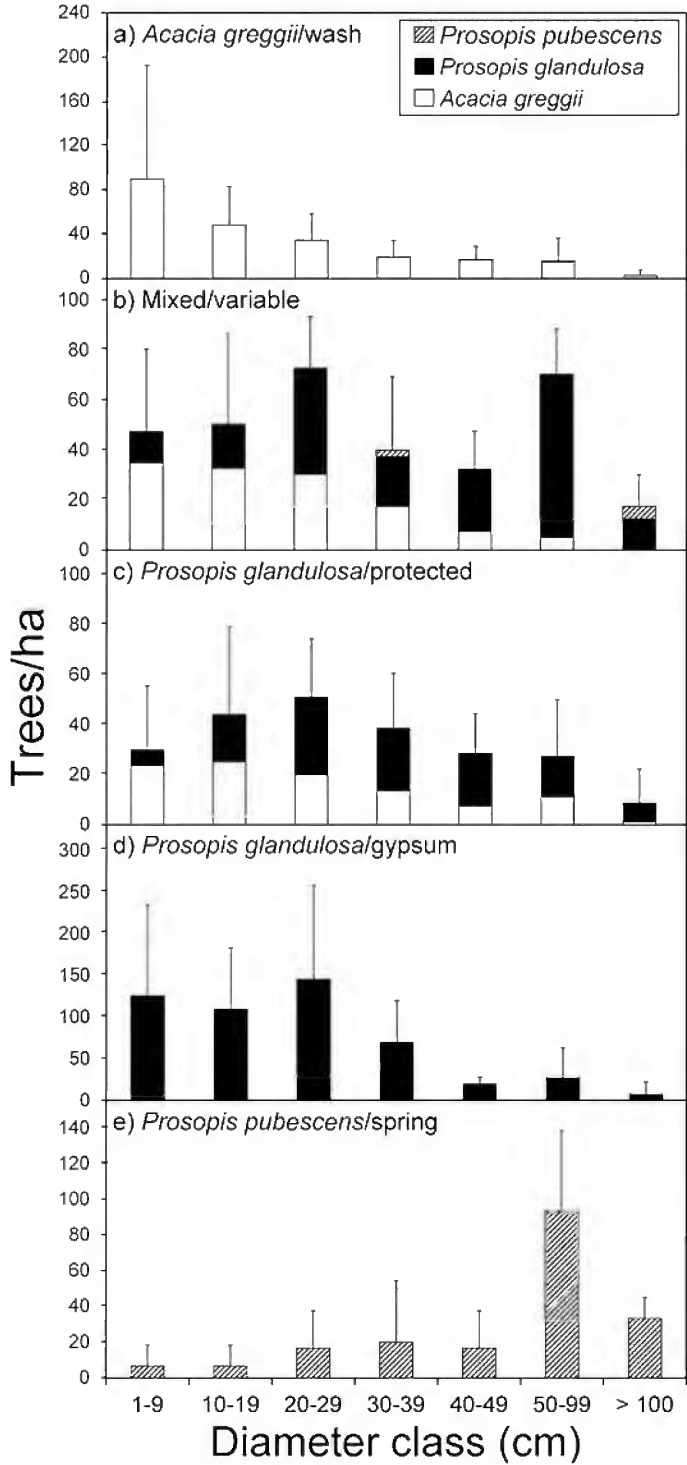


FIG. 8. Diameter at root collar distribution by tree species for *Acacia* and *Prosopis* community types of the eastern Mojave Desert, USA. Error bars are 1 SD. Note the difference in y-axis scales among the graphs.

m in summer 1992 to 1994 in the drainage of Sacatone Wash containing *Prosopis glandulosa* and *Prosopis pubescens* in the southern part of the study area (Inglis et al. 1996). In an area of the Bluepoint Spring outflow supporting *P. pubescens*, we also directly observed that depth to groundwater was approximately <2 m based on “sink-holes” where flowing groundwater was visible. Groundwater might be predicted to be deeper in *Acacia greggii* communities because they occupied dry washes characterized by more ephemeral, rather than perennial, water fluxes (Schwinning et al. 2011). Relationships of groundwater depth with *P. glandulosa* are unclear because some locales of this species were in topographically protected sites where shading might reduce evaporation and surface water might collect (Schwinning et al. 2011). Observed distributional differences in these communities afford opportunities for ecophysiological and hydrological research to improve understanding of habitat partitioning (Busch & Smith 1995). This is especially important for conservation given concerns about potential for groundwater pumping to lower regional water tables coupled with climate change (Deacon et al. 2007). Whereas Judd et al. (1971) concluded that established *P. glandulosa* could survive pumping-related lowering of water to 13 m below the surface before the trees died, Patten et al. (2008) suggest that declines in water depths of even a meter for near-surface groundwater can dramatically impact tree recruitment and associated species.

In addition to depth, groundwater chemistry might affect plant distribution by influencing composition of water that roots access (Springer et al. 2008). Near springs in Death Valley National Park in the western Mojave Desert, Hunt (1966) concluded that groundwater chemistry rather than soil chemistry more strongly correlated with distribution of *Prosopis glandulosa*.

Species Groups

Little research has examined ecological species groups in arid environments, but our results are consistent with some general principles of species groups in temperate regions. For instance, our finding that a species group was not restricted to one community type concurs with the common observation that most groups inhabit multiple communities but are quantitatively most abundant in only a few communities (Kashian et al. 2003). Species groups in temperate regions were more strongly correlated with multivariate environmental gradients than single-factor gradients (Goebel et al. 2001). We also found few strong correlations of groups with individual environmental variables, and occurrences instead were likely related to multivariate gradients in groundwater depth, chemistry, soil moisture under textural and topographic control, flooding frequency, and soil chemistry such as the presence of gypsum (Hunt 1966; Patten et al. 2008; Springer et al. 2008).

Obligate wetland species (e.g., *Juncus* and *Scirpus* spp.) were not well represented in the species groups or in the flora as a whole at these sites. Instead, the flora was dominated by species characterized as transitional between wetlands and uplands (Patten et al. 2008). Additionally, species of the *Acacia greggii*/wash community in particular are associated with disturbance. For example, abundance of *Hymenoclea salsola* and *Sphaeralcea ambigua* often increases following fire and other anthropogenic disturbances (Abella 2010), consistent with their occurrence in natural washes that are periodically disturbed by flooding.

Ecological Condition and Conservation Implications

Based on features of favored habitat described by Crampton and Sedinger (2011) for the conservation-priority bird *Phainopepla nitens*, many sites in the study area demonstrate favorable characteristics. Almost all nests of *P. nitens* are in mistletoe-infected trees (Crampton & Sedinger 2011), and we found that 66% of our 0.1-ha plots contained ≥ 1 infected tree. *Phainopepla nitens* nest suitability also is correlated with the number of infected trees, which we found averaged 62 ± 44 trees/ha on plots where mistletoe was present. Surveying abundance of *P. nitens* and other priority wildlife species across this network of woodland sites might help improve understanding of landscape-scale distributional relationships of wildlife species with plant communities.

Communities were dominated by native species, which comprised 94% of the total 201 taxa detected. In regression analysis, native species richness accounted for 22% of the variability in exotic richness, more than any other variable and consistent with the often-observed positive relationship between native and exotic richness (Tabacchi & Planty-Tabacchi 2005). The least species-rich community (*Prosopis pubescens*/spring) was least invaded, whereas the most species-rich sites generally were most invaded.

Of the 13 total exotic species detected, 3 are of greatest current concern to resource managers. *Bromus rubens* is a major concern because it increases fine fuel loads to facilitate spread of fire, which is a recent, novel disturbance to which native Mojave Desert flora is not considered well adapted (Abella 2010). At our study sites, however, *B. rubens* cover was low, exceeding 10% (and never more than 20% cover) at only 6 of its 43 occupied plots even including cover of dead stalks. Our study landscape as a whole is at a lower elevation than the middle elevations where *B. rubens* abundance is greatest in the Mojave Desert, suggesting that *B. rubens* even in riparian areas with supplemental moisture at low elevations does not attain the dominance it does in uplands at higher elevations (Abella et al. 2012b). Although we included dead plants as a measure of cumulative recent cover, *B. rubens* cover can vary dramatically between multi-year wet and dry periods (Steers et al. 2011) such that periodic monitoring of these riparian areas is warranted. The second species of greatest concern is *Brassica tournefortii*, which also can provide fuel and compete with native plants and predominates at low elevations (Barrows et al. 2009). We detected this species at only 3 sites, suggesting it is not presently a major component of these woodlands. The third species, *Tamarix ramosissima*, can outcompete native species and alter soil properties through production of salt-rich litter and exudates (Smith et al. 1998). Although we detected *T. ramosissima* at 22% of sites, this species and the native trees typically comprised different patches, as was also noted by Bagstad et al. (2006) along the San Pedro River in Arizona. Future management of this species might be guided by effectiveness of the biocontrol *Diorhabda carinulata* (tamarisk leaf beetle), presently moving south and reaching the northern boundary of the study area (Bateman et al. 2010). Although further monitoring is warranted, these riparian communities have lower exotic plant abundance in comparison to many other areas of the Mojave Desert including those that have burned by wildfire (Dudley 2009; Steers et al. 2011).

Other observations also suggested that threats to these woodlands were less prevalent in our study than observed in some other areas (Crampton et al. 2006). Qualitative observations indicated no evidence of fire or woodcutting at most sites, with only minimal (e.g., some branches) and localized cutting noted on plots near anthropogenic camping locations. Some observation of probable evidence (by recording browsed plants) of unauthorized livestock grazing was noted in the northeastern part of the study area, but effects to the woodlands are unclear. Lack of tree recruitment is considered a major problem in other areas (Crampton et al. 2006), but we observed tree densities well distributed among size classes, except in the *Prosopis pubescens*/spring community, which was dominated by large trees. Further investigation of recruitment potential in this community is warranted. If desired, it is feasible to actively facilitate establishment of *P. pubescens* and the other tree species through planting nursery grown seedlings (Abella & Newton 2009).

In summary, the data suggest that these woodlands were: readily classified into community types that might exhibit different conservation needs; correlated with some measured environmental variables, but further investigation into groundwater depth and chemistry could be informative; dominated by native species; inhabited by suites of annual and perennial plants classifiable into species groups displaying unique distributions; typified by well-distributed tree density across size classes at most sites; and characterized by low evidence of threats such as fire noted in other regions.

APPENDIX 1

Ecological species groups for *Acacia* and *Prosopis* woodlands of Lake Mead National Recreation Area, Mojave Desert, USA.

| Species group ^a | Community type | | | | |
|---|----------------------------|-----|-----|-----|-----|
| | AGW ^b | MV | PGP | PGG | PPS |
| <i>Acacia greggii</i> | Frequency (%) ^b | | | | |
| <i>Acacia greggii</i> —catclaw acacia | 100 | 100 | 70 | 25 | 0 |
| <i>Bromus arizonicus</i> —Arizona brome | 24 | 25 | 10 | 0 | 0 |
| <i>Camissonia boothii</i> —Booth's evening primrose | 21 | 0 | 0 | 0 | 0 |
| <i>Eriogonum palmerianum</i> —Palmer's buckwheat | 31 | 0 | 0 | 0 | 0 |
| <i>Erodium cicutarium</i> —redstem stork's bill* | 45 | 25 | 0 | 0 | 0 |

APPENDIX 1

Continued

| Species group ^a | Community type | | | | |
|--|----------------------------|-----|-----|-----|-----|
| | AGW ^b | MV | PGP | PGG | PPS |
| <i>Acacia greggii</i> | Frequency (%) ^b | | | | |
| <i>Hymenoclea salsola</i> ---cheesebush | 86 | 25 | 40 | 0 | 0 |
| <i>Pectocarya setosa</i> ---moth combseed | 21 | 0 | 0 | 0 | 0 |
| <i>Salvia columbariae</i> ---chia | 45 | 0 | 20 | 0 | 0 |
| <i>Eriogonum fasciculatum</i> | | | | | |
| <i>Eriogonum fasciculatum</i> ---eastern Mojave buckwheat | 55 | 50 | 10 | 0 | 0 |
| <i>Encelia virginensis</i> ---Virgin River brittlebush | 14 | 0 | 0 | 0 | 0 |
| <i>Phacelia vallis-mortae</i> ---Death Valley phacelia | 28 | 0 | 0 | 0 | 0 |
| <i>Porophyllum gracile</i> ---slender poreleaf | 21 | 25 | 0 | 0 | 0 |
| <i>Sphaeralcea ambigua</i> ---desert globemallow | 38 | 50 | 10 | 25 | 0 |
| <i>Xylorhiza tortifolia</i> ---Mojave woodyaster | 14 | 0 | 0 | 0 | 0 |
| <i>Ephedra viridis</i> | | | | | |
| <i>Ephedra viridis</i> ---mormon tea | 38 | 25 | 20 | 0 | 0 |
| <i>Amsinckia tessellata</i> ---bristly fiddleneck | 28 | 25 | 10 | 0 | 0 |
| <i>Draba cuneifolia</i> ---wedgeleaf draba | 10 | 50 | 0 | 0 | 0 |
| <i>Nemacladus glanduliferus</i> ---glandular threadplant | 14 | 25 | 0 | 0 | 0 |
| <i>Viguiera parishii</i> ---Parish's goldeneye | 21 | 50 | 10 | 0 | 0 |
| <i>Tamarix ramosissima</i> | | | | | |
| <i>Tamarix ramosissima</i> ---saltcedar* | 10 | 50 | 50 | 0 | 0 |
| <i>Funastrum cynanchoides</i> ---fringed twinevine | 3 | 0 | 30 | 0 | 0 |
| <i>Nicotiana obtusifolia</i> ---desert tobacco | 14 | 50 | 40 | 0 | 0 |
| <i>Stillingia linearifolia</i> ---queen's-root | 7 | 0 | 20 | 0 | 0 |
| <i>Ephedra torreyana</i> | | | | | |
| <i>Ephedra torreyana</i> ---Torrey's jointfir | 10 | 0 | 10 | 50 | 0 |
| <i>Bromus rubens</i> ---red brome* | 93 | 75 | 80 | 100 | 0 |
| <i>Chorizanthe brevicornu</i> ---brittle spineflower | 34 | 25 | 0 | 50 | 0 |
| <i>Cryptantha pterocarya</i> ---wingnut cryptantha | 24 | 25 | 0 | 50 | 0 |
| <i>Cuscuta denticulata</i> ---desert dodder | 17 | 25 | 0 | 25 | 0 |
| <i>Guillenia lasiophylla</i> ---California mustard | 14 | 0 | 0 | 75 | 67 |
| <i>Lepidium lasiocarpum</i> ---shaggyfruit pepperweed | 21 | 0 | 0 | 50 | 0 |
| <i>Schismus</i> spp.---Mediterranean grass* | 83 | 75 | 50 | 100 | 0 |
| <i>Ephedra nevadensis</i> | | | | | |
| <i>Ephedra nevadensis</i> ---Nevada jointfir | 21 | 0 | 20 | 0 | 0 |
| <i>Acamptopappus sphaerocephalus</i> ---rayless goldenhead | 14 | 0 | 0 | 0 | 0 |
| <i>Ambrosia eriocentra</i> ---woolly fruit bur ragweed | 17 | 0 | 10 | 0 | 0 |
| <i>Amsinckia menziesii</i> ---Menzies' fiddleneck | 14 | 0 | 20 | 0 | 0 |
| <i>Bromus tectorum</i> ---cheatgrass* | 14 | 0 | 0 | 0 | 0 |
| <i>Eriogonum thomasi</i> ---Thomas' buckwheat | 17 | 25 | 20 | 0 | 0 |
| <i>Pleuraphis rigida</i> ---big galleta | 10 | 50 | 0 | 0 | 0 |
| <i>Ericameria paniculata</i> | | | | | |
| <i>Ericameria paniculata</i> ---Mojave rabbitbrush | 14 | 25 | 20 | 0 | 0 |
| <i>Cryptantha circumsissa</i> ---cushion cryptantha | 28 | 0 | 0 | 0 | 0 |
| <i>Echinocereus engelmannii</i> ---hedgehog cactus | 7 | 50 | 20 | 0 | 0 |
| <i>Echinocereus polyacanthus</i> ---Mojave mound cactus | 3 | 50 | 10 | 0 | 0 |
| <i>Eriogonum deflexum</i> ---flatcrown buckwheat | 17 | 25 | 10 | 25 | 0 |
| <i>Yucca schidigera</i> ---Mojave yucca | 10 | 0 | 10 | 0 | 0 |
| <i>Larrea tridentata</i> | | | | | |
| <i>Larrea tridentata</i> ---creosote bush | 86 | 100 | 90 | 100 | 0 |
| <i>Cylindropuntia acanthocarpa</i> ---buckhorn cholla | 3 | 100 | 10 | 0 | 0 |
| <i>Eriogonum inflatum</i> ---desert trumpet | 21 | 75 | 20 | 75 | 0 |
| <i>Ferocactus cylindraceus</i> ---California barrel cactus | 7 | 75 | 10 | 0 | 0 |
| <i>Krameria erecta</i> ---littleleaf ratany | 14 | 50 | 0 | 75 | 0 |
| <i>Opuntia basilaris</i> ---beavertail pricklypear | 21 | 100 | 10 | 75 | 0 |
| <i>Encelia farinosa</i> | | | | | |
| <i>Encelia farinosa</i> ---brittlebush | 45 | 50 | 70 | 75 | 0 |
| <i>Bebbia juncea</i> ---sweetbush | 55 | 0 | 30 | 0 | 0 |

APPENDIX 1

Continued

| Species group ^a | Community type | | | | |
|--|----------------------------|-----|-----|-----|-----|
| | AGW ^b | MV | PGP | PGG | PPS |
| <i>Encelia farinosa</i> | Frequency (%) ^b | | | | |
| <i>Chamaesyce polycarpa</i> —smallseed sandmat | 45 | 25 | 20 | 25 | 0 |
| <i>Krameria grayi</i> —white ratany | 24 | 25 | 0 | 50 | 0 |
| <i>Stephanomeria pauciflora</i> —brownplume wirelettuce | 41 | 50 | 10 | 25 | 0 |
| <i>Ambrosia dumosa</i> | | | | | |
| <i>Ambrosia dumosa</i> —burrobush | 62 | 100 | 10 | 75 | 0 |
| <i>Polypogon monspeliensis</i> —annual rabbitsfoot grass | 3 | 50 | 20 | 0 | 0 |
| <i>Prosopis glandulosa</i> | | | | | |
| <i>Prosopis glandulosa</i> —honey mesquite | 3 | 100 | 100 | 100 | 33 |
| <i>Baccharis emoryi</i> —Emory's baccharis | 0 | 0 | 30 | 0 | 33 |
| <i>Pluchea sericea</i> | | | | | |
| <i>Pluchea sericea</i> —arrowweed | 7 | 25 | 40 | 0 | 67 |
| <i>Phragmites australis</i> —common reed | 0 | 25 | 20 | 0 | 33 |
| <i>Pleurocoronis plurisetia</i> —bush arrowleaf | 7 | 0 | 20 | 0 | 0 |
| <i>Suaeda moquinii</i> | | | | | |
| <i>Suaeda moquinii</i> —Mojave seablite | 0 | 0 | 0 | 100 | 67 |
| <i>Atriplex confertifolia</i> —shadscale saltbush | 0 | 0 | 0 | 75 | 33 |
| <i>Chorizanthe rigida</i> —devil's spineflower | 7 | 0 | 0 | 50 | 0 |
| <i>Descurainia pinnata</i> —western tansymustard | 34 | 50 | 50 | 75 | 33 |
| <i>Isocoma acradenia</i> —alkali goldenbush | 0 | 25 | 0 | 100 | 67 |
| <i>Plantago ovata</i> —desert Indianwheat | 17 | 50 | 10 | 75 | 0 |
| <i>Stylocine intertexta</i> —Morefield's neststraw | 7 | 0 | 0 | 75 | 0 |
| <i>Vulpia octoflora</i> —sixweeks fescue | 86 | 50 | 40 | 75 | 0 |
| <i>Allenrolfea occidentalis</i> | | | | | |
| <i>Allenrolfea occidentalis</i> —iodinebush | 0 | 0 | 0 | 25 | 100 |
| <i>Distichlis spicata</i> —saltgrass | 0 | 25 | 0 | 50 | 67 |
| <i>Prosopis pubescens</i> —screwbean mesquite | 0 | 25 | 0 | 0 | 100 |

^a Bold = perennial, not bold = annual or biennial, and * = exotic

^b Abbreviations and numbers of plots for community types: AGW = *Acacia greggii*/wash (n = 29), MV = Mixed/variable (n = 4), PGP = *Prosopis glandulosa*/protected (n = 10), PGG = *Prosopis glandulosa*/gypsum (n = 4), and PPS = *Prosopis pubescens*/spring (n = 3). Bold values signify where a species group is overall most frequent

ACKNOWLEDGMENTS

This study was funded through a cooperative agreement organized by Alice Newton between the National Park Service, Lake Mead National Recreation Area, and the University of Nevada Las Vegas (UNLV). We thank Joslyn Curtis and Sylvia Tran (UNLV) for help with fieldwork; Alice Newton and Dara Scherpenisse (LMNRA) for help with study design and insight on conservation implications; the UNLV Environmental Soil Analysis Laboratory (in particular Yuanxin Teng and Brenda Buck) for performing soil analyses; Sharon Altman (UNLV) for creating figures; and J. Andrew Alexander and Walter Fertig for helpful comments on the manuscript.

REFERENCES

- ABELLA, S.R. & W.W. COVINGTON. 2006. Vegetation-environment relationships and ecological species groups of an Arizona *Pinus ponderosa* landscape, USA. *Pl. Ecol.* 185:255–268.
- ABELLA, S.R. & A.C. NEWTON. 2009. A systematic review of species performance and treatment effectiveness for revegetation in the Mojave Desert, USA. In: A. Fernandez-Bernal and M.A. De La Rosa, eds. *Arid environments and wind erosion*. Nova Science Publishers, Inc., Hauppauge, New York. Pp. 45–74.
- ABELLA, S.R. 2010. Disturbance and plant succession in the Mojave and Sonoran Deserts of the American Southwest. *Int. J. Environ. Res. Public Health* 7:1248–1284.

- ABELLA, S.R., K.A. PRENGAMAN, T.M. EMBREY, S.M. SCHMID, A.C. NEWTON, & D.J. MERKLER. 2012a. A hierarchical analysis of vegetation on a Mojave Desert landscape, USA. *J. Arid Environm.* 78:135–143.
- ABELLA, S.R., T.M. EMBREY, S.M. SCHMID, & K.A. PRENGAMAN. 2012b. Biophysical correlates with the distribution of the invasive annual red brome (*Bromus rubens*) on a Mojave Desert landscape. *Invasive Pl. Sci. Managem.* 5:47–56.
- BAGSTAD, K.J., S.J. LITE, & J.C. STROMBERG. 2006. Vegetation, soils, and hydrogeomorphology of riparian patch types of a dryland river. *W. N. Amer. Naturalist* 66:23–44.
- BARROWS, C.W., E.B. ALLEN, M.L. BROOKS, & M.F. ALLEN. 2009. Effects of an invasive plant on a desert sand dune landscape. *Biol. Invas.* 11:673–686.
- BATEMAN, H.L., T.L. DUDLEY, D.W. BEAN, S.M. OSTOJA, K.R. HULTINE, & M.J. KUEHN. 2010. A river system to watch: Documenting the effects of saltcedar (*Tamarix* spp.) biocontrol in the Virgin River valley. *Ecol. Restorat. N. Amer.* 28:405–410.
- BEATLEY, J.C. 1966. Ecological status of introduced brome grasses (*Bromus* spp.) in desert vegetation of southern Nevada. *Ecology* 47:548–554.
- BEERS, T.W., P.E. DRESS, & L.C. WENSEL. 1966. Aspect transformation in site productivity research. *J. Forest.* (Washington, DC) 64:691–692.
- BREIMAN, L., J.H. FRIEDMAN, R.A. OLSHEN, & C.J. STONE. 1984. Classification and regression trees. Wadsworth, Inc., Belmont, California, USA.
- BURT, R., ED. 2004. Soil survey laboratory methods manual. Soil survey investigations rep. 42, vers. 4.0. U.S. Department of Agriculture, Natural Resources Conservation Service. U.S. Government Printing Office, Washington, D.C., USA.
- BUSCH, D.E. 1995. Effects of fire on southwestern riparian plant community structure. *S.W. Naturalist*. 40:259–267.
- BUSCH, D.E. & S.D. SMITH. 1995. Mechanisms associated with decline of woody species in riparian ecosystems of the southwestern U.S. *Ecol. Monogr.* 65:347–370.
- CAMPBELL, C.J. & W.A. DICK-PEDDIE. 1964. Comparison of phreatophyte communities of the Rio Grande in New Mexico. *Ecology* 45:492–502.
- CRAMPTON, L., J. KRUEGER, & D. MURPHY. 2006. Conservation management strategy for mesquite and acacia woodlands in Clark County, Nevada. Unpub. rep. submitted to Bureau of Land Management, Las Vegas Field Office, Nevada, USA.
- CRAMPTON, L. & J.S. SEDINGER. 2011. Nest-habitat selection by the phainopepla: Congruence across spatial scales but not habitat types. *Condor* 113:209–222.
- DALY, C., M. HALBLEIB, J.I. SMITH, W.P. GIBSON, M.K. DOGGETT, G.H. TAYLOR, J. CURTIS, & P.P. PASTERIS. 2008. Physiographically sensitive mapping of climatological temperature and precipitation across the conterminous United States. *Int. J. Climatol.* 28:2031–2064.
- DEACON, J.E., A.E. WILLIAMS, C.D. WILLIAMS, & J.E. WILLIAMS. 2007. Fueling population growth in Las Vegas: How large-scale groundwater withdrawal could burn regional biodiversity. *BioScience* 57:688–698.
- DUDLEY, T.L. 2009. Invasive plants in Mojave Desert riparian areas. In: R.H. Webb, L.F. Fenstermaker, J.S. Heaton, D.L. Hughson, E.V. McDonald, and D.M. Miller, eds. *The Mojave Desert: Ecosystem processes and sustainability*. University of Nevada Press, Reno, USA. Pp. 125–155.
- DUFRENE, M. & P. LEGENDRE. 1997. Species assemblages and indicator species: The need for a flexible asymmetrical approach. *Ecol. Monogr.* 67:345–366.
- EVENS, J.M. 2003. Vegetation in watercourses of the eastern Mojave Desert, California. In: P. Faber, ed. *California riparian systems: Processes and floodplains management, ecology, and restoration. 2001 riparian habitat and floodplains conference proceedings, riparian habitat joint venture, Sacramento, California, USA*. Pp. 106–115.
- GOEBEL, P.C., B.J. PALIK, L.K. KIRKMAN, M.B. DREW, L. WEST, & D.C. PEDERSON. 2001. Forest ecosystems of a Lower Gulf Coastal Plain landscape: Multifactor classification and analysis. *J. Torrey Bot. Soc.* 128:47–75.
- HAWKSWORTH, F.G. 1977. The 6-class dwarf mistletoe rating system. *Gen. Tech. Rep. RM-48*. U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado, USA.
- HUNT, C.B. 1966. Plant ecology of Death Valley. U.S. Geological Survey Professional Paper 509.
- INGLIS, R., C. DEUSER, & J. WAGNER. 1996. The effects of tamarisk removal on diurnal ground water fluctuations. *Tech. Rep. NPS/NRWRD/NRTR-96/93*. U.S. National Park Service, Washington, D.C., USA.
- JUDD, B.L., J.M. LAUGHLIN, H.R. GUENTHER, & R. HANDEGARDE. 1971. The lethal decline of mesquite on the Casa Grande National Monument. *Great Basin Nat.* 31:153–159.
- KASHIAN, D.M., B.V. BARNES, & W.S. WALKER. 2003. Ecological species groups of landform-level ecosystems dominated by jack pine in northern Lower Michigan, USA. *Pl. Ecol.* 166:75–91.
- KEELER-WOLF, T. 2007. Mojave Desert scrub vegetation. In: M.G. Barbour, T. Keeler-Wolf, and A.A. Schoenherr, eds. *Terrestrial vegetation of California*. University of California Press, Berkeley, USA. Pp. 609–656.

- LATO, L.J. 2006. Soil survey of Clark County area, Nevada. U.S. Department of Agriculture, Natural Resources Conservation Service. U.S. Government Printing Office, Washington, D.C., USA.
- MCCUNE, B. & M.J. MEFFORD. 1999. PC-ORD: Multivariate analysis of ecological data. Vers. 4. User's guide. MjM Software Design, Gleneden Beach, Oregon, USA.
- MCCUNE, B., R. ROSENRETER, J.M. PONZETTI, & D.C. SHAW. 2000. Epiphyte habitats in and old conifer forest in western Washington, USA. *Bryologist* 103:417–427.
- MEYER, S.E. 1986. The ecology of gypsophile endemism in the eastern Mojave Desert. *Ecology* 67:1303–1313.
- MILLER, D., S.R. ARCHER, S.F. ZITZER, & M.T. LONGNECKER. 2001. Annual rainfall, topographic heterogeneity and growth of an arid land tree (*Prosopis glandulosa*). *J. Arid Environm.* 48:23–33.
- PATTEN, D.T., L. ROUSE, & J.C. STROMBERG. 2008. Isolated spring wetlands in the Great Basin and Mojave Deserts, USA: Potential response of vegetation to groundwater withdrawal. *Environm. Managem.* 41:398–413.
- SADA, D.W., J.E. WILLIAMS, J.C. SILVEY, A. HALFORD, J. RAMAKKA, P. SUMMERS, & L. LEWIS. 2001. A guide to managing, restoring, and conserving springs in the western United States. Tech. Ref. 1737-17. Bureau of Land Management, National Science and Technology Center, Denver, Colorado, USA.
- SAS INSTITUTE. 2009. SAS/STAT 9.2 user's guide. SAS Institute, Cary, North Carolina, USA.
- SAS INSTITUTE. 2010. Using JMP 9. SAS Institute, Cary, North Carolina, USA.
- SCHWINNING, S., D.R. SANDQUIST, D.M. MILLER, D.R. BEDFORD, S.L. PHILLIPS, & J. BELNAP. 2011. The influence of stream channels on distributions of *Larrea tridentata* and *Ambrosia dumosa* in the Mojave Desert, CA, USA: Patterns, mechanisms and effects of stream redistribution. *Ecology* 4:12–25.
- SMITH, S.D., D.A. DEVITT, A. SALA, J.R. CLEVERLY, & D.E. BUSCH. 1998. Water relations of riparian plants from warm desert regions. *Wetlands* 18:687–696.
- SPRINGER, A.E., L.E. STEVENS, D.E. ANDERSON, R.A. PARNELL, D.K. KREAMER, L.A. LEVIN, & S.P. FLORA. 2008. A comprehensive springs classification system: Integrating geomorphic, hydrogeochemical, and ecological criteria. In: L.E. Stevens and V.J. Meretsky, eds. *Aridland springs in North America: Ecology and conservation*. University of Arizona Press and Arizona-Sonora Desert Museum, Tucson. Pp. 49–75.
- STEERS, R.J., J.L. FUNK, & E.B. ALLEN. 2011. Can resource-use traits predict native vs. exotic plant success in carbon amended soils? *Ecol. Applic.* 21:1211–1224.
- STROMBERG, J.C. 1993. Riparian mesquite forests: A review of their ecology, threats, and recovery potential. *J. Arizona-Nevada Acad. Sci.* 27:111–124.
- TABACCHI, E. & A. PLANTY-TABACCHI. 2005. Exotic and native plant community distributions within complex riparian landscapes: A positive correlation. *Ecoscience* 12:412–423.
- TAN, K.H. 2005. Soil sampling, preparation, and analysis. CRC Press, Boca Raton, Florida.
- THOMAS, K.A., T. KEELER-WOLF, J. FRANKLIN, & P. STINE. 2004. Mojave Desert ecosystem program: Central Mojave vegetation mapping database. U.S. Geological Survey, Western Regional Science Center and Southwest Biological Science Center, Flagstaff, Arizona, USA.
- USDA, NRCS [Natural Resources Conservation Service]. 2012. The PLANTS database. National Plant Data Center, Baton Rouge, Louisiana. <http://plants.usda.gov>. Accessed 15 August 2012.
- WATSON, D.M. 2001. Mistletoe – a keystone resource in forests and woodlands worldwide. *Ann. Rev. Ecol. Syst.* 32:219–249.